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CHEMICAL ECOLOGY OF THE HETEROPTERA¹

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INTRODUCTION

True bugs are probably best known as stink bugs because nearly all Heterop-
tera have scent glands (27, 150). In fact, their overwhelming chemical
fortification confounds the task of isolating sex pheromones (151). This
review emphasizes recent pheromonal research for the group, as well as
newly identified and unusual heteropteran allomones. Contact chemorecep-
tion and nutrition are not discussed (143). Readers can consult reviews for
details on heteropteran venoms (134), alarm pheromones (27), and scent
gland histology and morphology (34, 40, 150).

Heteropteran Families

The heteropteran taxa are treated in reverse phylogenetic order, beginning
with families of the terrestrial infraorders Pentatomomorpha and Cimicomor-
pha, followed by the primarily aquatic Nepomorpha, and ending with the few
pertinent works on semiaquatic bugs (Amphibicorisae) and the terrestrial
Enicocephalomorpha (135).

COREIDAE This is the squash bug family. Larvae of these large plant-
feeding bugs have dorsal abdominal scent glands (DAGs) opening between
tergites 4/5 and 5/6 (40). The DAGs are cuticle-lined sacs, with gland cells
forming the gland wall. At metamorphosis the DAGs in coreids (but not all
bugs) are lost, and the metathoracic scent gland (MTG), opening laterally

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between the meso- and metathoracic legs, becomes functional. However, its gland cells are segregated from the reservoir wall; each of a pair of massive accessory glands (AG_1 s, lateral glands) empties into the reservoir via a duct, and there is another pair of small accessory glands (AG_2 s) that are outgrowths of the reservoir wall (Figure 1) (7, 34). In the ancestral condition of the heteropteran MTG the gland cells lie in the reservoir wall (as in larval DAGs) and there is a single midventral opening (34). The more derived condition is segregation of gland cells from the reservoir (as in coreids), division of the reservoir, reduction in gland size, and loss of the AG_2 s (34). Some (perhaps most) male and female coreids and others of the lineage possess extra exocrine glands associated with the genitalia, referred to here as ventral abdominal glands (164).

The DAG exudates of coreid larvae contain the C_6 , and in some species the C_8 , α,β -unsaturated aldehydes (*E*)-2-hexenal and (*E*)-2-octenal, plus 4-oxo-(*E*)-2-hexenal (26). Often the corresponding alcohols are present in smaller quantities (26), but esters and/or acids have been reported for this larval secretion in only two coreids (26, 44).

The complexity of the MTG in coreids is chemically reflected in the secretion. MTG secretions are mixtures of saturated or α,β -unsaturated aldehydes, alcohols, acetate or butyrate esters of these alcohols, and C_2 , C_4 , or C_6 acids (26, 86). These blends are at most genus specific (6, 172). Variations in the proportions of aldehydes and esters (e.g. 32) are due in part to compartmentalized biosynthesis (7). In the leafhopper bug, *Leptoglossus phyllopus*, hexyl acetate is secreted by the AG_1 s into the reservoir, where

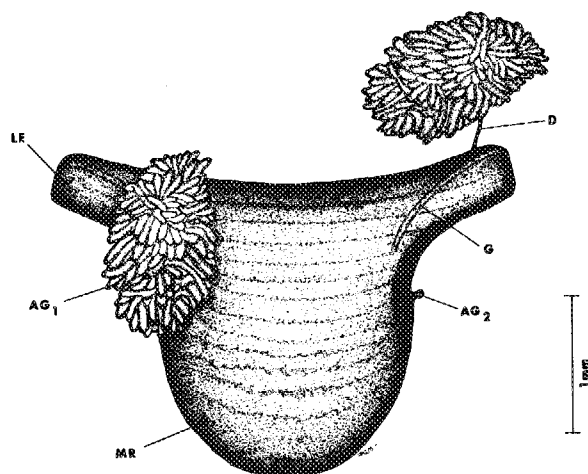


Figure 1 The metathoracic scent gland of *Leptoglossus phyllopus*. AG_1 , primary accessory gland; AG_2 , secondary accessory gland; D, duct; G, chitinous groove; LE, lateral extension; MR, median reservoir.

esterase and dehydrogenase cleave the ester and oxidize it spontaneously to produce a condensation product (Figure 2). If AG_2 s are absent, the ultimate scent of a species from a related family of leafhoppers cannot explain all components of the MTG secretion of *Holopogon* (150). Increase in age (150) and adult scent secretions of *Holopogon* include acetaldehyde, but the increase is not significant (44).

Male ventral abdominal glands have been analyzed (Figure 2). They dominate these species-specific odors with the odors of 5-14, but aliphatic alcohols and esters. Males of the large territory species secrete esters, including tiglates and other compounds from abdominal glands in females. Males of *Holopogon* secrete volatile compounds (J. R. Aldrich, unpublished). Parasitic species secrete specific odor, as males of

ALYDIDAE Broadheaded bugs. The larvae are remarkable for their scent glands. Larvae possess DAGs and secrete a scent. Larval scents include (*E*)-2-octenal and other unsaturated aldehydes. They are rancid: Butyric and hexanoic acids, butyrate, hexanol, and methylbutanoic acids dominate the scent of *Megalotomus* (Figure 2). MTG secretions, and the AG_2 s are absent. Ventral abdominal glands were found in *Alydus* or

RHOPALIDAE "Scentless" bugs. Some of the Rhopalinae are scentless (8). Adults of the other rhopalids secrete

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ected in the α, β -unsaturated ls, and C_2 , C_4 , cific (6, 172). are due in part y, *Leptoglossus* reservoir, where

esterase and dehydrogenase enzymes, apparently secreted by the AG_2 s, cleave the ester and oxidize the resulting alcohol. Further reactions occur spontaneously to produce hexanoic acid, hexanal trimer, and an aldol condensation product (Figure 2, 1, 2) (7). In one coreid species in which the AG_2 s are absent, the ultimate secretion is >90% hexyl acetate. The MTG in a species from a related family, Hyocephalidae, has an extra pair of accessory glands and secretes virtually pure hexanal (168). This biosynthetic scheme cannot explain all compositional variations, however. For example, in the MTG secretion of *Holopterna allata* males, the concentrations of some esters increase with age (150). The occurrence of 3-hydroxybutanal in larval and adult scent secretions of a South African coreid may be due to condensation of acetaldehyde, but the inclusion of 2-hexanol is inexplicable (Figure 2, 3, 4) (44).

Male ventral abdominal gland secretions for 10 coreids from four genera have been analyzed (Figure 2, 5-16, 18-23) (5, 6, 11, 64). Aromatics dominate these species-specific secretions in *Leptoglossus* and include compounds with the odors of cherries, vanilla, cinnamon, and roses (Figure 2, 5-14), but aliphatic alcohols and esters also occur (Figure 2, 15, 16, 18, 19). Males of the large territorial coreid *Pachylis laticornis* produce exclusively esters, including tiglates and a benzoate (Figure 2, 20-23) (11). Ventral abdominal glands in females, when present, apparently do not produce volatile compounds (J. R. Aldrich, unpublished). In addition, airborne trapping experiments with field-collected *Leptoglossus oppositus* adults revealed that males vent cyclic sesquiterpenes never observed from females (J. R. Aldrich, unpublished). Parasitic tachinid flies apparently home in on some male-specific odor, as males are more heavily parasitized than females (6).

ALYDIDAE Broadheaded bugs are closely related to coreids, and in many the larvae are remarkable ant mimics and the imagoes are wasplike (149). Larvae possess DAGs and an MTG as Coreidae do, but lack the AG_2 s (112). Larval scents include (*E*)-2-hexenal and 4-oxo-(*E*)-2-hexenal, plus traces of (*E*)-2-octenal and other unidentified compounds (17). Alydid MTG secretions are rancid: Butyric and hexanoic acids dominate with lesser amounts of hexyl butyrate, hexanol, and hexanal in *Alydus*; butyric, isobutyric, and 2-methylbutanoic acids dominate with corresponding aldehydes and esters in *Megalotomus* (Figure 2, 24-31) (17). Branched compounds are unusual for MTG secretions, and the preponderance of acids is difficult to rationalize if AG_2 s are absent. Ventral abdominal glands occur in alydids (164), but none were found in *Alydus* or *Megalotomus* (J. R. Aldrich, unpublished).

RHOPALIDAE "Scentless" plant bugs supposedly lack the MTG, but at least some of the Rhopalinae actually possess an MTG resembling that of coreids (8). Adults of the other rhopalid subfamily (Serinethinae) exhibit the derived

primary accessory
lar extension; MR,

condition of divided and extremely reduced MTGs (34), but retain one or both of the DAGs (8; J. R. Aldrich, unpublished). All rhopalid males examined have ventral abdominal glands (164).

The 4/5 DAG secretion of the adult rophaline *Niesthrea louisianica* contains perilla alcohol (Figure 2, 32) plus (*E*)-2-hexenal and an unidentified hydrocarbon (larval DAGs have not been analyzed) (8). The MTG secretion is

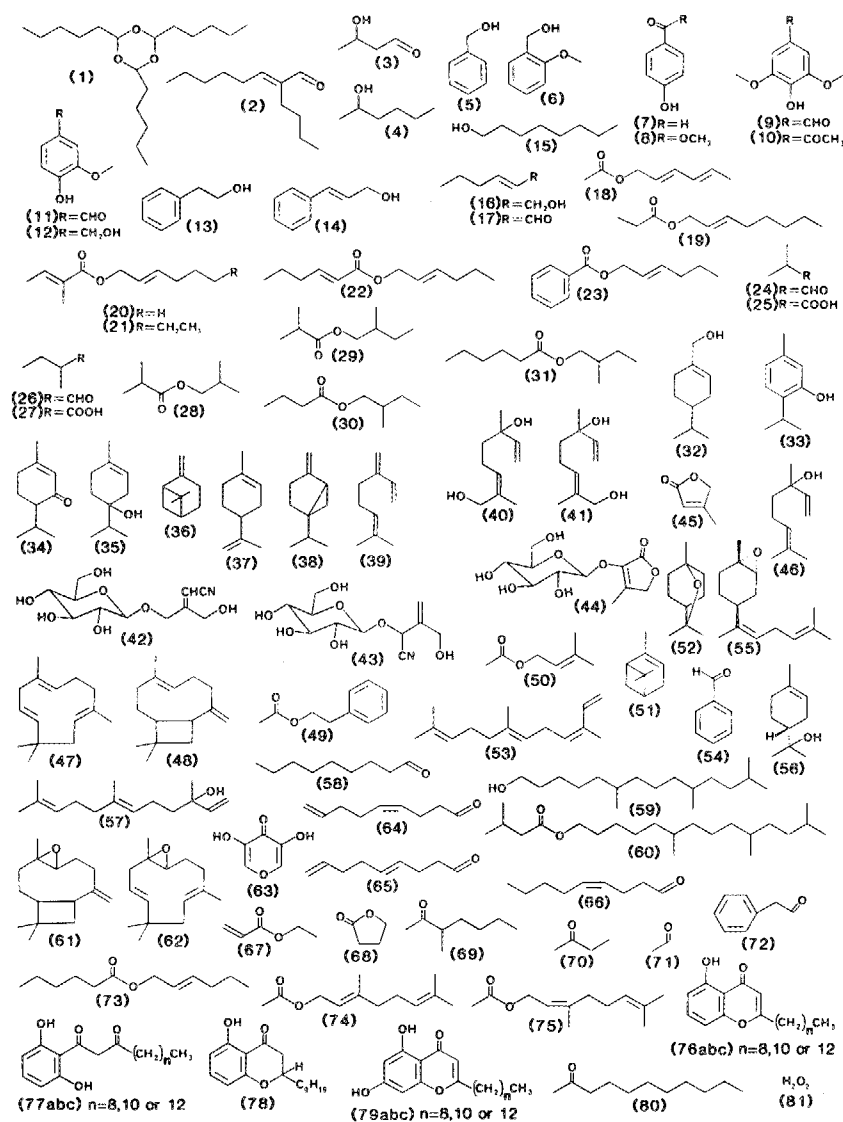
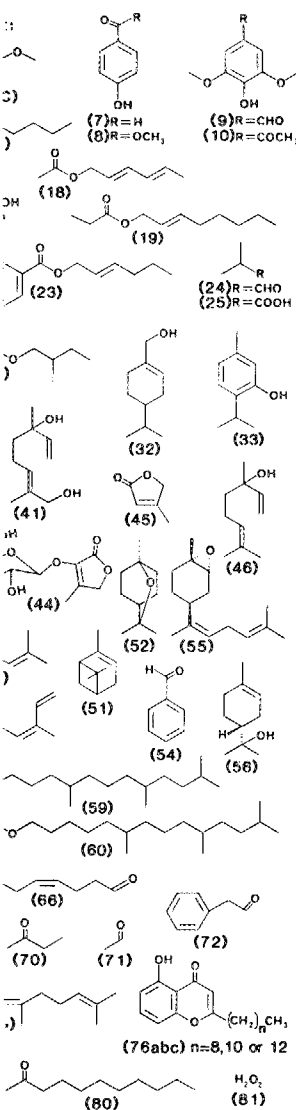


Figure 2 Unusual excretory glands; l-DG, larval dorsal abdominal gland; BG, body hemolymph; EX, excretory [77], (4) 2-n-butyloct-2-enol [(44)], (2) 2-hexanol [MT (6)], (6) guaiacol [VG (5, 6)], (11) hydroxybenzoate [VG (6)], (5, 6), (11) vanillin [VG (6)], (6, 64)], (14) cinnamaldehyde [VG (64), a-DG (14, 69)], (17) [VG (64), MT (59, 69)], (11)], (21) (E)-2-octenyl benzoate [VG (26)], (26) 2-methylbutyl isobutyrate [MT (17)], (2) [MT (17)], (31) 2-methylbutyl isobutyrate [MT (8)], (34) piperitone, β -pinene [MT (8, 69), l-DG (8)], (38) sabinene [l-DG (8)], myrcene [MT (8), l-DG (8)], (J. R. Aldrich, unpublished), (6) glucopyranosyloxy-3-hydroxy-3- β -D-glucopyranosyloxy- (J. R. Aldrich, unpublished), α -humulene [AS (J. P. Farrell, unpublished), l-DG (65)], [MT (155)], (51) α -pinene farnesene [MT (88)], (54) bisabolene [SG (16a, 21)], (58) nonanal [a-DG (15, 69)], trimethyltetradecyl isovaleryl humulene epoxide II [l-DG (66)], (67) ethyl acrylate [UK (16)], [MT (128)], (70) 2-butanone phenylacetaldehyde [MT (70, 71)], (75) neryl acetate [MT (117)], (77abc) 1-(3,3-dimethylchromanone) [SS (11)], undecanone [SS (116)].

(34), but retain one or both
l rhopalid males examined

Niesthrea louisianica con-
sexual and an unidentified
(8). The MTG secretion is



devoid of aliphatic carbonyls and is instead a blend of monoterpenes (Figure 2, 33–37) (8). Ventral abdominal glands are highly developed (J. R. Aldrich, unpublished), but have yet to be analyzed.

Exocrines from six serinethine species have been analyzed (8; J. R. Aldrich, unpublished). (*E*)-2-Hexenal, (*E*)-2-octenal, and 4-oxo-(*E*)-2-

Figure 2 Unusual exocrine compounds of Heteroptera and their sources (MT, metathoracic glands; l-DG, larval dorsal abdominal glands; a-DG, adult dorsal abdominal glands; VG, ventral abdominal gland; BG, Brindley's gland; SG, sternal glands; AS, abdominal sternum; H, hemolymph; EX, excreta; SS, secretory setae; UK, unknown source). (1) hexanal trimer [MT (7)], (2) 2-*n*-butyloct-2-enal [MT (7, 26), l-DG (26)], (3) 3-hydroxybutanal [MT (44), l-DG (44)], (4) 2-hexanol [MT (44), l-DG (44)], (5) benzyl alcohol [VG (5, 6, 64), a-DG (9, 10, 14)], (6) guaiacol [VG (5, 6)], (7) *p*-hydroxybenzaldehyde [VG (6), MT (26)], (8) methyl *p*-hydroxybenzoate [VG (6), MT (26)], (9) syringaldehyde [VG (5, 6)], (10) acetosyringone [VG (5, 6)], (11) vanillin [VG (5, 6), UK (165)], (12) vanillyl alcohol [VG (6)], (13) 2-phenylethanol [VG (6, 64)], (14) cinnamyl alcohol [VG (6)], (15) 1-octanol [VG (6)], (16) (*E*)-2-hexenol [VG (64), a-DG (14, 69)], (17) (*E*)-2-hexenal [a-DG (8, 9, 14, 15)], (18) (*E,E*)-2,4-hexadienyl acetate [VG (64), MT (59, 69)], (19) 2-octenyl propionate [VG (64)], (20) (*E*)-2-hexenyl tiglate [VG (11)], (21) (*E*)-2-octenyl tiglate [VG (11)], (22) (*E*)-2-hexenyl (*E*)-2-hexenoate [VG (11)], (23) (*E*)-2-hexenyl benzoate [VG (11)], (24) isobutanal [MT (17)], (25) isobutyric acid [MT (17), BR (26)], (26) 2-methylbutanal [MT (17)], (27) 2-methylbutanoic acid [MT (17)], (28) isobutyl isobutyrate [MT (17)], (29) 2-methylbutyl isobutyrate [MT (17)], (30) 2-methylbutyl butyrate [MT (17)], (31) 2-methylbutyl hexanoate [MT (17)], (32) perilla alcohol [a-DG (8)], (33) thymol [MT (8)], (34) piperitone [MT (8)], (35) terpinen-4-ol [MT (8, 115), a-DG (9, 10, 14)], (36) β -pinene [MT (8, 69), l-DG (65), a-DG (8)], (37) limonene [MT (8, 69, 115), l-DG (65), a-DG (8)], (38) sabinene [l-DG (J. R. Aldrich, unpublished), a-DG (J. R. Aldrich, unpublished)], (39) myrcene [MT (8), l-DG (J. R. Aldrich, unpublished), a-DG (8)], (40) (*Z*)-linalool diol [VG (J. R. Aldrich, unpublished)], (41) (*E*)-linalool diol [VG (J. R. Aldrich, unpublished)], (42) 4- β -D-glucopyranosyloxy-3-hydroxymethyl-2-butenylnitrile [H (29)], (43) cardiospermin [H (29)], (44) 3- β -D-glucopyranosyloxy-4-methyl-2(5H)-furanone [H (29)], (45) 4-methyl-2(5H)-furanone [EX (J. R. Aldrich, unpublished)], (46) linalool [MT (42, 53), l-DG (12), a-DG (9, 10, 14)], (47) α -humulene [AS (J. P. Farine, unpublished), l-DG (65)], (48) β -caryophyllene [AS (J. P. Farine, unpublished), l-DG (65)], (49) 2-phenethyl acetate [MT (155)], (50) 3-methyl-2-butenyl acetate [MT (155)], (51) α -pinene [MT (115), l-DG (65)], (52) 1,8-cineole [MT (115)], (53) (*Z,E*)- α -farnesene [MT (88)], (54) benzaldehyde [l-DG (15), a-DG (14, 15)], (55) (*Z*)-3,4-epoxy- α -bisabolene [SG (16a, 21)], (56) *R*-(+)- α -terpineol [a-DG (9, 10)], (57) nerolidol [a-DG (14)], (58) nonanal [a-DG (15, 63)], (59) 6,10,13-trimethyltetradecanol [SG (13, 16)], (60) 6,10,13-trimethyltetradecyl isovalerate [SG (13, 16)], (61) caryophyllene oxide [l-DG (65)], (62) humulene epoxide II [l-DG (65)], (63) 3,5-dihydroxy-4-pyrone [SG (89)], (64) (*Z*)-4,8-nonadienal [a-DG (63)], (65) (*E*)-4,8-nonadienal [a-DG (63)], (66) (*Z*)-4-nonenal [a-DG (63)], (67) ethyl acrylate [UK (167)], (68) γ -butyrolactone [MT/EX? (114)], (69) 3-methyl-2-hexanone [MT (128)], (70) 2-butanone [MT (26), l-DG (26)], (71) acetaldehyde [MT (26), l-DG (26)], (72) phenylacetaldehyde [MT? (67)], (73) (*E*)-2-hexenyl hexanoate [MT (87)], (74) geranyl acetate [MT (70, 71)], (75) neryl acetate [MT (70, 71)], (76abc) 2-alkyl-5-hydroxychromones [SS (116, 117)], (77abc) 2-(1,3-diketoalkyl)-resorcinols [SS (116, 117)], (78) 5-hydroxy-2-nonylchromanone [SS (116)], (79abc) 2-alkyl-5,7-dihydroxychromones [SS (117)], (80) 2-undecanone [SS (116)], (81) hydrogen peroxide [MT (26)].

octenal comprise >90% of the 4/5 DAG secretions of all *Jadera* adults and larvae; however, the imaginal secretions contain less (*E*)-2-hexenal than do larval secretions. The exudate from the larval 4/5 DAG of boxelder bugs, *L. trivittatus*, is similar to the *Jadera* secretions, except 4-oxo-(*E*)-2-hexenal replaces (*E*)-2-hexenal. The 4/5 DAG is missing in *Leptocoris* adults. The 5/6 DAG exudate consists of pleasant-smelling monoterpenes (Figure 2, 36–39), and although the blends from adults and larvae within a species are indistinguishable, these blends are quantitatively different among *Jadera* species. The ventral abdominal glands of *Leptocoris* males smell like roses, producing pure 2-phenylethanol (Figure 2, 13), whereas *Jadera* males secrete linalool diol, the *Z*-isomer (two species), or the *E*-isomer (one species) (Figure 2, 40, 41) plus unidentified compounds.

Serinethines are vividly colored and show a decided preference (132) for toxic cyanolipid-containing seeds of the Sapindaceae (29, 38a). Coincidentally, certain conspicuous leaffooted coreids [e.g. *Anisocelis* (108)] are host specific on cyanogenic Passifloraceae (132). Serinethines convert cyanolipids to cyanogenic glucosides that are sequestered and that can be externalized by bleeding through weak points in the cuticle (29; J. R. Aldrich, unpublished). Adult and larval *Jadera* and larvae of *Leptocoris isolata* (29) that are fed sapindaceous seeds containing fatty acid esters of 2-hydroxy-3-(hydroxymethyl)-3-butenitrile sequester the cyanoglucosides 4- β -D-glucopyranosyloxy-3-hydroxymethyl-2-butenitrile and cardiospermin (Figure 2, 42, 43). However, in adult *L. isolata* the lactonic glucoside 3- β -D-glucopyranosyloxy-4-methyl-2(5H)-furanone (Figure 2, 44) replaces cardiospermin (29). *Jadera* adults and larvae fed sapindaceous seeds containing 4-hydroxy-3-(hydroxymethyl)-2-butenitrile sequester the first of the above cyanoglucosides and excrete 4-methyl-2(5H)-furanone (Figure 2, 45). *Jadera* release HCN when crushed in the presence of a β -glucosidase preparation (J. R. Aldrich, unpublished).

PYRRHOCORIDAE Red bugs or cotton stainers specialize on Malvales (58), and toxic gossypol pigments in cottonseed might be the basis for the bugs' aposematism. Larvae possess three DAGs, and the anterior two glands continue to function in adults (150). The MTG and AG₂s are reduced (derived condition), and in some species (e.g. *Dysdercus intermedius*) the reservoir is completely divided (34). In male *Dysdercus* adults the fifth abdominal sternite has many more epidermal glands than in female adults (91). *Dysdercus cingulatus* males reportedly have a ventral abdominal gland (J. P. Farine, unpublished).

The anterior DAGs are tiny, and except for the presence of tetradecane (26) their chemistry is unknown. In *Pyrrhocoris apterus* larvae the posterior DAG secretes (*E*)-2-octenal and 4-oxo-(*E*)-2-octenal (153); in *Dysdercus* this secre-

tion contains (*E*)-2-hexenal (42). Irritated larvae use the posterior DAG, which spreads over the body.

In *D. intermedius*, the posterior DAG is involved in synthesizing (*E*)-2-hexenal and storing linalool (Figure 2, 40). In *Dysdercus*, as these aldehydes are absent from *D. supersticiosus fasciatus* (129a). In *D. intermedius* a female odor stimulus is 65% *S*-(+)-linalool and 35% β -humulene (J. P. Farine, unpublished).

BERYTIDAE Stilt bugs (130), but their secretions are not known. They show a striking preference for scavenging on entrapped insects, reduced or absent (40). Their bodies, which are

LYGAEIDAE Scent glands are present in over 2700 species of stink bugs on the MTG chemistry. The presence of (*E*)-2-hexenal is characteristic of the Rhyparochrominae (whose scent gland secretion is plant and thus may be scent-oriented ground-dwelling seed bugs. Virtually all are aposematically colored. Lygaeines contain cardiotonic lygaeines such as the sequestration system in the layered epidermis in which the chemical cost. These chemical insects are squeezed (milkweed bugs contain 137). Rhyparochrominae in their odors (161). The

of all *Jadera* adults and less (*E*)-2-hexenal than do DAG of boxelder bugs, *L. leptocoris* adults. The 5/6 rpenes (Figure 2, 36-39), within a species are in-erent among *Jadera* spe-ales smell like roses, reas *Jadera* males secrete *E*-isomer (one species)

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tion contains (*E*)-2-hexenal, 4-oxo-(*E*)-2-hexenal, hexanal, and tridecane (26, 42). Irritated larvae usually excrete urine first and then the contents of the 5/6 DAG, which spread over the aqueous urine (150).

In *D. intermedius*, 1-4 days after adult emergence the AG₁s switch from synthesizing (*E*)-2-hexenyl and (*E*)-2-octenyl acetate to synthesizing and storing linalool (Figure 2, 46) (53). This may be characteristic of the genus *Dysdercus*, as these aliphatics coexist with linalool in extracts of whole MTGs from *D. supersticiosus* (42), *D. cingulatus* (J. P. Farine, unpublished), and *D. fasciatus* (129a). In *D. similis* (68), *D. koenigii* (73), and *D. cingulatus* (138) a female odor stimulates male courtship. In the last species, females produce 65% *S*-(+)-linalool and 35% *R*-(-)-linalool (129a). The sesquiterpene hydrocarbons β -humulene and β -caryophyllene (Figure 2, 47, 48) have also been isolated from the abdominal sternites of male *D. cingulatus* (J. P. Farine, unpublished).

BERYTIDAE Stilt bugs have enormous spouts associated with their MTGs (130), but their secretions have not been chemically investigated. Berytids show a striking preference for feeding on sticky plants, and they often scavenge on entrapped insects or are predatory (171). Larval DAGs are reduced or absent (40), but many early-stage berytids have glandular hairs on their bodies, which bear sticky droplets (149).

LYGAEIDAE Scent gland chemistry has been examined for just five of the over 2700 species of seed bugs (144). Among these analyses a cursory report on the MTG chemistry of one predatory species, *Geocoris varius*, noted the presence of (*E*)-2-hexenal, (*E*)-2-decenal, and tridecane (172). Brown, somber bugs that feed on fallen seeds constitute the largest subfamily, the Rhyparochrominae (~1200 species) (161). However, the seed-feeding bugs whose scent gland secretions have been analyzed feed on seeds still on the plant and thus may be prey to sight-oriented aerial predators instead of scent-oriented ground predators (130). The Lygaeinae are the most advanced seed bugs. Virtually this entire assemblage feeds on toxic Apocynales. Many are aposematically colored, and the MTG is reduced (130, 136). All stages of lygaeines contain cardiac glycosides originating from host plants (166). In lygaeines such as the large milkweed bug, *Oncopeltus fasciatus*, the sequestration system is specialized to the extent that adults have a double-layered epidermis in which cardenolides accumulate at little or no physiological cost. These chemicals are emitted through cuticular weak points when the insects are squeezed (137). Moreover, the DAG and MTG secretions from milkweed bugs contain cardenolides in admixture with aliphatic carbonyls (137). Rhyparochromines have an acrid taste quite independent of variations in their odors (161). The Insectivora (e.g. shrews) are important predators in

litter, and as most nonprimate mammals are color-blind, the scents of ground-dwelling lygaeids may serve as the aposematic signals associated by vertebrates with poisons. Indeed, there is evidence in *O. fasciatus* for de novo synthesis of histamine or an analog (66).

Larval DAG secretions contain C_6 , C_8 , and C_{10} alk-2-enals, C_6 and C_8 4-oxo-alk-2-enals, and sometimes alkanes (26, 155, 156). The proportions of the higher-molecular weight components are greater in the posterior DAG secretions, and emission from this gland is usually simultaneous with excretion of urine (150, 156). Some sphecoid wasps provision their nests with heteropteran larvae, and a cuckoo wasp oviposits in *Nysius* lygaeid larvae as a means of ultimately parasitizing its sphecoid host (37). The extent to which these wasps use DAG scents to find prey is unknown.

The MTG chemistry of seed bugs is extraordinary. In milkweed bugs the secretion is sexually dimorphic: Males release a blend of C_6 and C_8 alk-2-enyl and alka-2,4-dienyl acetates (e.g. Figure 2, 18) with lesser amounts of the corresponding aldehydes, but females release almost purely the aldehydes (59). The difference is explained by the apparent existence of a valve in males that prevents the AG_1 -secreted esters from entering the median reservoir until the moment of release (54, 152). Isolated male milkweed bugs smell sweet, in contrast to isolated females (92). In *Spilostethus rivularis* (Lygaeinae) the MTG is reduced and divided, the AG_2 s are not evident, and the secretion is sexually dimorphic (155). Both sexes secrete (*E,E*)-2,4-hexadienyl acetate and 2-phenethyl acetate (Figure 2, 18, 49), but the former constitutes 96% of the male secretion versus only a trace of the female secretion, and the latter accounts for 2% of the male secretion but 13% of the female secretion (155). (*E*)-2-Octenyl acetate (51%) is the major female secretory constituent, and 3-methylbutyl acetate and 3-methyl-2-butenyl acetate (Figure 2, 50) are abundant and exclusively female natural products (155). Both sexes of the cotton seed bug, *Oxycarenus hyalinipennis* (Oxycareninae), express an age-dependent switch from synthesizing aliphatics to synthesizing isoprenoids in the MTG (88, 115), reminiscent of cotton stainers (53). During the first day of adult life, the AG_1 s secrete (*E*)-2-hexenyl and (*E*)-2-octenyl acetates into the reservoir. There the corresponding aldehydes and 4-oxo-alkenals are derived (presumably via AG_2 enzymes), although significant quantities of octenyl acetate persist (115). In both sexes, after day 1 the AG_1 s abruptly switch to isoprenoid synthesis and swell with mono- and sesquiterpenes (Figure 2, 37, 51-53) (88, 115). Handling of the bugs elicits ejection of terpenes in admixture with carbonyls, accompanied by an audible stridulation (88, 115).

Some lygaeine males have ventral abdominal glands that open one segment posterior to those of coreoids (164), but extracts of this gland from *O. fasciatus* showed no sign of volatiles by gas chromatography (J. R. Aldrich, unpublished). All oxycarenine males have sternal setal patches, which probably secrete some kind of pheromone (36).

PENTATOMIDAE The t developed DAGs and M line to the Coreoidea from upper parts of plants. S glands defy his predict frequent this biotope. T *rydema* spp. are interesti ic, and have reduced M sequester mustard oil gly liberate the heteropteran pentatomid MTG is of th embedded in the reservo many species, perhaps remain active in adults.

The posterior DAGs and sometimes C_{10} alk-2 other alkanes (26). The larval DAGs (99) is alme spined soldier bug, *Poc octenal, and tridecane p DAGs (Figure 2, 54). (Figure 2, 46) from the along with 4-oxo-(*E*)-2- Linalool isolated from sp (-)-linalool (129a). Exu ent monoterpenols, rend*

Pentatomid MTG secr and C_8 (but not C_{10}) 4-o the alk-2-enols (26, 79, MTG secretory pattern, final secretion is enzym esters (15, 150). Kleptor bugs caught in spiderwe

Male *N. viridula* prod from the tiny 3/4 DAGs hexenal, hexanal, and he the long-range attractan *Nezara* pheromone as a from Florida failed to p that the pheromone of Hawaiian *N. viridula*. N nal sternites that are vis males of the European

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PENTATOMIDAE The true stink bugs, as their name suggests, have highly developed DAGs and MTGs. Pentatomids and allied families are a parallel line to the Coreoidea from a lygaeid-like ancestor. Most stink bugs feed on the upper parts of plants. Schaefer (130) found that their well-developed scent glands defy his prediction that the MTG might be reduced in bugs that frequent this biotope. The harlequin bug, *Murgantia histrionica*, and *Eurydema* spp. are interesting exceptions: They feed on crucifers, are aposematic, and have reduced MTGs (105, 130, 149). One can guess that they sequester mustard oil glycosides such as sinigrin, and that when attacked they liberate the heteropteran version of war gas, allyl isothiocyanate (26). The pentatomid MTG is of the coreid type except that the AG_2 is a band of tissue embedded in the reservoir wall (150). Larvae have 4/5 and 5/6 DAGs, but many species, perhaps most, also possess a pair of minute 3/4 DAGs that remain active in adults.

The posterior DAGs of larval phytophagous pentatomids secrete C_6 , C_8 , and sometimes C_{10} alk-2-enals, C_6 and C_8 4-oxo-alkenals, and tridecane and other alkanes (26). The 4-oxo-(*Z*)-2-hexenal reported from *Nezara viridula* larval DAGs (99) is almost certainly the *E*-isomer. Larvae of the predaceous spined soldier bug, *Podisus maculiventris*, produce (*E*)-2-hexenal, (*E*)-2-octenal, and tridecane plus heretofore unrecorded benzaldehyde in their 3/4 DAGs (Figure 2, 54). Even more surprising is the discovery of linalool (Figure 2, 46) from the 4/5 and 5/6 DAG discharges of *P. maculiventris*, along with 4-oxo-(*E*)-2-hexenal, tridecane, and a trace of tetradecanal (12). Linalool isolated from spined soldier bug larvae is a 97/3 blend of *S*-(+)-/*R*-(−)-linalool (129a). Exudates from two other *Podisus* species include different monoterpenols, rendering the secretions species-specific (129a).

Pentatomid MTG secretions are rich in alkanes, C_8 and C_{10} alk-2-enals, C_6 and C_8 (but not C_{10}) 4-oxo-alkenals, and lower concentrations of acetates of the alk-2-enols (26, 79, 81, 113). The spined soldier bug exhibits the same MTG secretory pattern, plus a trace of linalool (Figure 2, 46) (12, 15). The final secretion is enzymatically derived in the reservoir from AG_1 -secreted esters (15, 150). Kleptoparasitic milichiid flies are drawn to the odor of stink bugs caught in spiderwebs (142).

Male *N. viridula* produce an attractant pheromone (16a, 72). Compounds from the tiny 3/4 DAGs in adults have been characterized [tridecane, (*E*)-2-hexenal, hexanal, and hexanol (9)], but this slightly dimorphic secretion is not the long-range attractant. The tachinid fly *Trichopoda pennipes* uses the *Nezara* pheromone as a kairomone (16a, 72); however, *T. pennipes* imported from Florida failed to parasitize *N. viridula* in Hawaii (39), which suggests that the pheromone of *N. viridula* from Florida is different from that of Hawaiian *N. viridula*. *Nezara* males have areas on their two anterior abdominal sternites that are visibly smoother than the surrounding cuticle (35), and males of the European strain excrete a pair of sesquiterpene isomers from

these areas that were attractive to conspecific females in an olfactometer (121). However, males of the Brazilian *Nezara* strain secrete a single sesquiterpene epoxide (Figure 2, 55) that was attractive to females of this strain in a laboratory bioassay (21). Airborne extracts of *Nezara* males from the southern United States contained both the *trans*-isomer identified from the Brazilian strain (Figure 2, 55) and the *cis*-isomer in a 3:1 ratio (16a).

Many male predaceous pentatomids (Asopinae) have enormous 3/4 DAGs or glandular setal patches on the sternum (10, 13, 14, 16). In *P. maculiventris* the DAG secretion [(*E*)-2-hexenal (45%), *R*-(+)- α -terpineol (45%), benzyl alcohol (6%), terpinen-4-ol, and linalool (Figure 2, 17, 56, 5, 35, 46), plus traces of *trans*- and *cis*-piperitol (9, 10)] is a powerful attractant. *S*-(--)- α -Terpineol is inactive but not inhibitory, and an effective artificial pheromone can be prepared from (*E*)-2-hexenal and racemic α -terpineol (1:2 volume ratio) (14). The pheromone of a sympatric species, *Podisus fretus*, has also been deciphered: *S*-(+)-linalool (49%), (*E*)-2-hexenal (35%), benzyl alcohol (12%), nerolidol (2%), and α -terpineol (1%) (Figure 2, 46, 17, 5, 57, 56), plus traces of several alcoholic compounds (14). An artificial pheromone can be made by mixing (*E*)-2-hexenal and (\pm)-linalool (1:2 volume ratio) (14). A hybrid pheromone consisting of hexenal, α -terpineol, and linalool (1:1:1 volume ratio) attracts both *Podisus* species (J. R. Aldrich, unpublished). The small 3/4 DAGs of *P. maculiventris* females produce their own unique blend: (*E*)-2-hexenal and the acid, with traces of benzaldehyde and nonanal (Figure 2, 54, 58) (12, 15). Females of the scelionid egg parasitoid, *Telenomus calvus*, seem to use both sex-specific soldier bug odors as cues; parasitoids are attracted to calling males, but only become phoretic on female bugs (3). Enlarged DAGs occur in males from at least two other asopine genera (*Zicrona* and *Alcaeorhynchus*) (9). However, in species of the asopines *Stiretrus*, *Perillus*, *Oplomus*, and *Mineus*, males possess pubescent patches on sternites 4-6 (13, 16); when starved and then fed coccinellid or chrysomelid beetle prey, these bugs secrete 6,10,13-trimethyltetradecanol and/or the isovalerate ester of this norterpenol (Figure 2, 59, 60) (13, 16). The asopine genera *Picromerus*, *Dinorhynchus*, *Apateticus*, and *Euthyrhynchus* have neither sexually dimorphic DAGs nor sternal glands (J. R. Aldrich, unpublished). Certain phytophagous pentatomids that are occasionally predaceous (e.g. *Brochymena*) (105) are among the stink bugs whose males and females secrete a powdery wax over the sternum (93).

SCUTELLERIDAE Shield bugs are always phytophagous and resemble stink bugs in the arrangement and chemistry of their MTG and larval DAGs (40, 150). (*E*)-2-Decenal and 4-oxo-(*E*)-2-hexenal (plus tridecane in larvae) are common secretory components (65, 69, 147). One cotton-feeding species, *Hotea gambiae*, can be added to the mushrooming list of bugs that synthesize

terpenes; β -pinene and MTG secretory constituents of larvae produce exclusives 48, 51, 61, 62) (65). The terpenes are absent from 16) (69).

Some shield bugs (Tetrascleridae) while in others the strigolactone. In male cotton harlequin (130), and in virgin male deposit of 3,5-dihydroxy-2-hexanone have large 3/4 DAGs thymol (Figure 2, 58, 64). *Eurygaster integriceps* has presumably other compounds (165, 167).

PLATASPIDAE The scutellerids, to the extreme (108) resembling those of their MTG and DAGs (86, 172). Males have sternal glands (35).

CYDNIDAE Burrowing bugs (105). Their wing venation generally matching the pattern of alk-2-enals were mistaken for γ -butyrolactone in the (Figure 2, 68) (114), a metabolite like the lactone exocrine glands have no

ACANTHOSOMATIDAE Bugs (105, 107), and the larvae deposit trail pheromones. Acanthosomatid females probably involved in guarding scattered over their sternum

REDUVIIDAE AND PHYCETOPHAGIDAE Wait predators belonging

females in an olfactometer strain secrete a single ses-
 tive to females of this strain
 s of *Nezara* males from the
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 mer in a 3:1 ratio (16a).

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ophagous and resemble stink
 MTG and larval DAGs (40,
 plus tridecane in larvae) are
 One cotton-feeding species,
 ug list of bugs that synthesize

terpenes; β -pinene and limonene (Figure 2, 36, 37) coexist with the usual
 MTG secretory constituents in adults (69), whereas the paired anterior DAGs
 of larvae produce exclusively mono- and sesquiterpenes (Figure 2, 36, 37, 47,
 48, 51, 61, 62) (65). The 3/4 DAGs are proportionally larger in adult males
 than in larvae, whereas in females they regress in size; but in both sexes
 terpenes are absent from adults and (*E*)-2-hexenol is predominant (Figure 2,
 16) (69).

Some shield bugs (Tetyrinae) have stridulatory areas on sternites 4–6 (145),
 while in others the strigils are replaced by pubescent sternal glands (35, 36).
 In male cotton harlequin bugs, *Tectacoris diophthalmus*, the MTG is reduced
 (130), and in virgin males the sternal glands are often loaded with a crystalline
 deposit of 3,5-dihydroxy-4-pyrone (Figure 2, 63) (89). *Sphaerocoris* males
 have large 3/4 DAGs that release an odoriferous array of C₉ aliphatic alde-
 hydes (Figure 2, 58, 64–66) (63). Finally, calling males of the wheat pest
Eurygaster integriceps liberate vanillin, ethyl acrylate (Figure 2, 11, 67), and
 presumably other compounds, but the source of these volatiles is unknown
 (165, 167).

PLATASPIDAE The scutellum is even more enlarged in these bugs than in
 scutellerids, to the extreme that some males have elaborate pronotal horns
 (108) resembling those of certain territorial beetles (163). What little is known
 of their MTG and DAG exocrines conforms to the general pentatomid pattern
 (86, 172). Males have sternal glands (108) or dorsally situated integumental
 glands (35).

CYDNIDAE Burrower bugs are fossorial but have been collected from an
 airplane (105). Their well-developed MTG and DAGs produce exocrines
 generally matching the pentatomoid pattern (26). It seems likely that 4-oxo-
 alk-2-enals were mistaken for quinones in one species (129). The occurrence
 of γ -butyrolactone in the MTG secretion of *Aethus indicus* is also exceptional
 (Figure 2, 68) (114), but it is possible that this lactone is an excretory
 metabolite like the lactone from rhopalids (Figure 2, 45). Sexually dimorphic
 exocrine glands have not been noticed in cydnids.

ACANTHOSOMATIDAE Parental care is common for these pentatomid-like
 bugs (105, 107), and they are semiochemically adapted to this life mode;
 larvae deposit trail pheromones and emit alarm pheromones (27, 102). Some
 acanthosomatid females have setal patches on sternite 7 (124), which are
 probably involved in guarding eggs. Males have integumental exocrine glands
 scattered over their sternum (35).

REDUVIIDAE AND PHYMATIDAE Assassin and ambush bugs are sit-and-
 wait predators belonging to the terrestrial infraorder Cimicomorpha (135,

145). The sedentary mode of capturing prey and the use of the rostrum for stinging defense (134) seem to have contributed to the reduction of the MTG and DAGs and to the evolution of new exocrine glands (34, 40, 150). Thus, in most reduviids and phymatids the MTG is either a small, divided gland without AG₂s or is missing (150). Concurrently, two pairs of saclike glands have arisen: (a) Brindley's glands situated laterally under the first abdominal tergite, and (b) ventral glands at the junction of the thorax and abdomen (150). The new glands and the MTGs sometimes coexist (e.g. *Phymata* spp. have both ventral and Brindley's glands), but Brindley's glands are rarely absent (34). Secretions from Brindley's glands in hematophagous reduviids (Triatominae) consist primarily of isobutyric acid (Figure 2, 25) (26). Brindley's glands are missing in one triatomine species, *Dipetalogaster maximus*, but MTGs are retained and secrete 3-methyl-2-hexanone (Figure 2, 69) (128). Ventral gland secretions have not been analyzed, nor have the larval or the occasionally functional adult DAGs (34, 40).

Females of Harpactocorinae have evolved subrectal exocrine glands that are odoriferous in at least some species (43). In wheel bugs, *Arilus cristatus*, (J. R. Aldrich, unpublished), and the South American *Arilus carinatus* (23) a bright orange subrectal gland with a nauseatingly sweet odor is everted like a caterpillar osmeterium when the bugs are disturbed.

Many reduviids have glandular setae that produce viscid fluids (108). Pilose areas on the fore-tibiae of some reduviids (and Nabidae), designated fossula spongiosae, secrete a sticky substance used to grasp prey (108). Larvae and sometimes adult reduviines have dorsal abdominal setae that exude glutinous material, which the insects use to stick bits of debris on themselves for camouflage (101, 108). Apiomerinae collect resin from plants instead of secreting it, and smear the gathered material onto their forelegs (108). The advantage of using plant resin rather than resin synthesized de novo appears to involve aggressive chemical mimicry; bees are attracted by the odor of plant resin, which often proves fatal when the source is a cataleptic assassin bug (108, 169). Milichiid flies are also attracted to the vicinity by the plant-derived resin and swoop down to lap the blood of captured prey (142). Aggressive chemical mimicry has been reported for the reduviid *Ptilocerus ochraceus*, whose adults and larvae ooze a sweet but intoxicating fluid from a sternal gland, which attracts and then paralyzes ants (150). It has been suggested that the unusual bananalike odor from another reduviid entices fruit flies to their unsuspecting deaths (101).

CIMICIDAE All that is known of the semiochemicals of these blood-sucking ectoparasites of cavernicolous birds and mammals concerns the bed bug, *Cimex lectularius* (150). This age-old pest has a somewhat reduced MTG with a single AG₂ and three small larval DAGs (34, 40). The secretions contain C₆

and C₈ alk-2-enals, but also (26). Larval secretions are and the mixture releases exists (particularly powerful (27).

ANTHOCORIDAE Little is predators. MTG and larva unique 4/5 ventral abdomi

MIRIDAE Mirids typically resource these small plant largest of all heteropteran aphids and other phloem-feeding solely prey on these insect defenses of plant bugs, but the rectum as a holdfast of acetaldehyde (Figure 2, meadow plant bugs (26). *St. lineolaris*, contained mostly and 10:1 in females and males (Figure 2, 72) and an undecyl use the scent of *Lygus* bugs and hexyl butyrate are major predaceous *Pilophorus per* component are present only in mainly hexyl and (E)-2-hex feeding mirid, *Harpocera* a sex-specific pattern similar secretory components of mirid with geranyl and neryl acet contains more of the correct DAG secretions have not been the fact that braconid parasitism tarnished plant bug exuviae secretion of mirid larvae contents are shed with the

Various Bryocorinae feed coffee, cocoa, and cola), (94). Curiously, the bryocorid lost the MTG, and although has no external opening (2

and the use of the rostrum for to the reduction of the MTG glands (34, 40, 150). Thus, in other a small, divided gland, two pairs of saclike glands ally under the first abdominal of the thorax and abdomen s coexist (e.g. *Phymata* spp. Brindley's glands are rarely in hematophagous reduviids d (Figure 2, 25) (26). Brind- es, *Dipetalogaster maximus*, xanone (Figure 2, 69) (128). d, nor have the larval or the

subrectal exocrine glands that wheel bugs, *Arilus cristatus*, African *Arilus carinatus* (23) and; sweet odor is everted like a thread.

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D). The secretions contain C₆

and C₈ alk-2-enals, but also 2-butanone and acetaldehyde (Figure 2, 70, 71) (26). Larval secretions are enriched in higher-molecular weight components, and the mixture releases alarm behavior (27). An assembling pheromone exists (particularly powerful for adults), but it remains chemically unknown (27).

ANTHOCORIDAE Little is known of the semiochemistry of these important predators. MTG and larval DAGs are present, and some males possess a unique 4/5 ventral abdominal gland (34, 123).

MIRIDAE Mirids typically suck the juices of meristematic plant tissue, a resource these small plant bugs have luxuriantly exploited to become the largest of all heteropterans families (145, 149). However, as competitors of aphids and other phloem-feeding homopterans, many mirids occasionally or solely prey on these insects. Crypsis and mimicry are common first-line defenses of plant bugs, backed up by agile escape maneuvers or extrusion of the rectum as a holdfast organ (96, 149, 170). (*E*)-2-Octenyl acetate and acetaldehyde (Figure 2, 71) were identified from adult steam-distilled meadow plant bugs (26). Steam distillates of adult tarnished plant bugs, *Lygus lineolaris*, contained mostly hexyl butyrate and (*E*)-2-hexenyl butyrate (1:1 and 10:1 in females and males, respectively), but also phenylacetaldehyde (Figure 2, 72) and an unidentified C₁₅ alcohol (67). Kleptoparasitic milichiids use the scent of *Lygus* bugs captured by spiders as a kairomone (142). Butyl and hexyl butyrates are major components from the MTG secretion of the predaceous *Pilophorus perplexus*, and octyl acetate and an unidentified component are present only in females. Another predatory mirid produces primarily hexyl and (*E*)-2-hexenyl hexanoate (Figure 2, 73) (87). An oak-feeding mirid, *Harpocera thoracica*, produces only terpenoids in its MTG in a sex-specific pattern similar to, but the reverse of, that of the aliphatic MTG secretory components of milkweed bugs: The female secretion is enhanced with geranyl and neryl acetate (Figure 2, 74, 75), and the male secretion contains more of the corresponding aldehydes and alcohols (70, 71). Larval DAG secretions have not been chemically analyzed for any mirids. However, the fact that braconid parasitoids seize and attempt to oviposit in larval tarnished plant bug exuviae (97) suggests that parasitoids use the DAG secretion of mirid larvae as a host-finding cue (in Heteroptera the DAG contents are shed with the cast skin).

Various Bryocorinae feed on a group of botanically diverse plants (tea, coffee, cocoa, and cola), all of which contain methylpurines (e.g. caffeine) (94). Curiously, the bryocorines that feed on these alkaloid-rich plants have lost the MTG, and although a 3/4 DAG is present in both larvae and adults, it has no external opening (20). When larvae are disturbed, the DAG is pul-

sated, and drops of fluid simultaneously exude from setae over their bodies (20). One can speculate that these bugs sequester host-plant alkaloids in the DAG and deliver them when needed via the blood or an epidermal syncytium (as in milkweed bugs) to setae or cuticular weak points.

Caged *Lygus*, *Lygocoris*, *Distantiella*, and *Helopeltis* females release a pheromone that is attractive to flying males (28, 65a, 85, 146, 150). Neither the source nor the identity of any of these pheromones is known, but the spermatheca was postulated as the source of pheromone in *Lygus hesperus* (158). This is a plausible origin because in mirids the spermatheca does not store sperm and is probably not a cement gland (as in reduviids), as mirids insert their eggs into plants (158).

TINGIDAE Most of the 1800 species of lace bugs feed underneath leaves on mesophyll and a few develop inside galls, but the feeding habits of myrmecophilous tingids are unknown (49). The MTG of foliar and gall-making lace bugs is divided and reduced (34, 150); however, the myrmecophiles have extensive areas of modified cuticle surrounding the MTG openings (49). Tingid MTG and DAG secretions have not been analyzed chemically.

The larvae of foliar lace bugs are frequently armed with spiny tubercles that make them look as weird as the reticulated adults. Many larvae are equipped with glandular setae that bear droplets (49, 98). Larval droplets from two *Stephanitis* species contain novel 2-alkyl-5-hydroxy- and 2-alkyl-5,7-dihydroxychromones, plus some of the corresponding chromanones and diketones (Figure 2, 76–79) (116, 117). Decanal and 2-undecanone (Figure 2, 80) were also identified in droplets from *S. pyrioides* (116). In their immature stages, *Paracopium* and *Copium* species are protected inside galls and lack both spiny tubercles and glandular setae (49). *Gargaphia* species have spines, but descriptions of maternal care in *Gargaphia* do not mention secretory setae (84, 162). Larvae of *Corythuca* and the semisocial *Gargaphia solani* become alarmed when a nearby conspecific larva or a larva of one of the other species is crushed (84).

PLEIDAE Pigmy backswimmers are water bugs of the almost exclusively predaceous infraorder Nepomorpha (135). Pleid larvae have a 3/4 DAG, and adults have a saclike MTG with a single midventral opening (40). *Plea leachi* occasionally leaves the water and spreads hydrogen peroxide (Figure 2, 81) and carbonyl compounds from the MTG over the body with its legs (150).

NOTONECTIDAE The DAGs are absent in all backswimmers, and the MTG is missing in one subfamily. Notonectinae have a midventrally opening MTG with paired AG₁s (but without AG₂s) that in one species secrete p-

hydroxybenzaldehyde and (157).

NAUCORIDAE Creeping stink bugs. The MTG secretion is identified from *Notonecta*

CORIXIDAE Water boatmen. Three DAGs and adults have three glands may be retained by solid material such as algae or rostrum for defense (145). Other water bugs (157), corixids, secrete 4-oxo-alk-2-enals; the C₆ and C₈ compound predominate. Larvae eject jets of DAG secretion over the MTG

GELASTOCORIDAE Toad bugs. Terrestrial predators around water. Absent in Nerthrinae but present in all other larvae (40). Contains principally 4-oxo-

BELOSTOMATIDAE Giant water bugs. The backwaters of streams. (145). The DAGs are missing in the Belostomatidae. The MTG, its morphology is different. AG₁s synthesize and store butyrate (40, 157). Furthermore, females (157). In 1957, a component from the MTG secretion has since been identified as butyrate is a minor component of (E)-2-hexenyl esters in this obscure group of true bugs. Availability of *Lethocerus* for seasoning for fatty foods. Fluid when attacked (96).

AMPHIBICORISAE The Heteroptera living on or

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d or an epidermal syncytium
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elopeltis females release a
65a, 85, 146, 150). Neither
omones is known, but the
romone in *Lygus hesperus*
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(as in reduviids), as mirids

s feed underneath leaves on
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0); however, the myrmeco-
surrounding the MTG open-
o not been analyzed chemi-

ed with spiny tubercles that
. Many larvae are equipped
. Larval droplets from two
ydroxy- and 2-alkyl-5,7-
ling chromanones and dike-
t-undecanone (Figure 2, 80)
s (116). In their immature
ected inside galls and lack
gargaphia species have spines,
not mention secretory setae
l *Gargaphia solani* become
a of one of the other species

of the almost exclusively
larvae have a 3/4 DAG, and
al opening (40). *Plea leachi*
en peroxide (Figure 2, 81)
e body with its legs (150).

ekswimmers, and the MTG
midventrally opening MTG
n one species secrete *p-*

hydroxybenzaldehyde and methyl *p*-hydroxybenzoate (Figure 2, 7, 8) (150, 157).

NAUCORIDAE Creeping water bugs have exocrine glands as in notonectines. The MTG secretion of *Ilyocoris cimicoides* contains the same phenolics identified from *Notonecta* (Figure 2, 7, 8) (150).

CORIXIDAE Water boatmen are unusual nepomorphans in that larvae have three DAGs and adults have a large MTG (40, 157). Well-developed scent glands may be retained because corixids are the only bugs known to ingest solid material such as algae and mosquito larvae and are unable to use the rostrum for defense (145). Notwithstanding their morphological similarity to other water bugs (157), corixids have MTG and DAG secretions composed of 4-oxo-alk-2-enals; the C₆ compound is predominant in the adult secretion and the C₈ compound predominates in that of larvae (26, 154). When attacked, larvae eject jets of DAG fluid under water, and adults extrude a drop of secretion over the MTG opening (154).

GELASTOCORIDAE Toad bugs deviate from other nepomorphans in being terrestrial predators around the edges of streams and ponds (157). The MTG is absent in Nerthrinae but well developed in Gelastocorinae, and DAGs are absent from all larvae (40, 157). The MTG secretion of *Gelastocoris oculatus* contains principally 4-oxo-2-hexenal (60%) and 2-octenal (25%) (26).

BELOSTOMATIDAE Giant water bugs are the insect sharks of ponds, lakes, and the backwaters of streams, feeding on small fish and aquatic insects (145). The DAGs are missing in all belostomatids (40), and the MTG is lacking in the Belostomatinae (157). Although the Lethocerinae have an MTG, its morphology is unique: The median reservoir is missing, paired AG₁s synthesize and store secretion, and each AG₁ opens via a midventral duct (40, 157). Furthermore, the glands are massive in males but minute in females (157). In 1957, (*E*)-2-hexenyl acetate was identified as the principal component from the MTG secretion of *Lethocerus indicus* males. This acetate has since been identified from *Lethocerus* females, and the corresponding butyrate is a minor component in the secretion from males (26). The function of (*E*)-2-hexenyl esters in *Lethocerus* remains unknown (150). Research on this obscure group of tropical water bugs was promoted by the commercial availability of *Lethocerus* extract in Southeast Asia, where it is used as a seasoning for fatty foods. Some belostomatids squirt a noxious inky black fluid when attacked (96).

AMPHIBICORISAE The Amphibicorisae is one of Dufour's subdivisions for Heteroptera living on or around water. The group is now divided into three

monophyletic infraorders, including predators such as shore bugs (Saldidae) and water striders (Gerridae and Veliidae) (135). Larvae run the gamut from having no DAG (water striders) to having four DAGs (Dipsocoridae), and the MTGs (when present) are more often than not confusing combinations of derived and reduced structures (40). Some shore bugs have even evolved osmeteria in addition to their MTGs (48). The small water striders can instantly double their speed by exuding saliva, which breaks the surface tension of the water behind them (19). The widespread occurrence of communication via waves in aquatic and semiaquatic Heteroptera (1) may explain the frequent loss of exocrine glands in these bugs.

ENICOCEPHALIDAE This is the sole family in an infraorder considered the sister group to the other six heteropteran infraorders (135). Unique-headed bugs are rare terrestrial predators (77) and are the only bugs that form airborne swarms that serve as mating leks (159, 163). Individual genera create male-dominated, female-dominated, or mixed swarms, with male-dominated swarms possibly most common (159). Males often have larger eyes than females (90). The 3/4 DAG of larvae remains active in both sexes of adults. The MTG has only been found in males, where it has a peculiar tubular form (34, 40).

DEFENSE

Defensive secretions can be classified as nonspecific irritants, specific toxins, and entangling substances (119). Small arthropods are vulnerable to entanglement, irritants are effective against arthropod predators, and poisons are the best chemical defense against birds and other vertebrates (119). The MTG and larval DAG secretions of terrestrial Heteroptera are primarily defensive irritants (127, 150). Larval allomones are enriched in high-molecular weight constituents, presumably because the flightless immatures require longer-lasting protection (17, 26, 150). The secretions of ground-dwelling imagoes often resemble those of larvae in this respect (26). Besides serving as solvents that modulate evaporation of volatile irritants, alkanes (and possibly esters in coreids) act synergistically as spreading and penetrating agents (127, 150). The phenolics and hydrogen peroxide of aquatic bugs are secondarily evolved MTG secretions that are probably important as antiseptics (150).

Ants are a major threat to bugs (95). (*E*)-2-Hexenal, hexanal, hexanol, hexanoic acid, 2-butyl-2-octenal, β -pinene, limonene, and farnesenes are ant alarm or trail pheromones emitted by various heteropterans for defense (27). The ubiquitous 4-oxo-alk-2-enals may effectively mimic ketonic formicid pheromones and the entire battery of heteropteran scent-gland weapons may have evolved to mimic ant pheromones as a result of selection pressure by

ants. The phenomenon was the same (Wasmannian mimicry) and morphological resemblance a dubious explanation for mimicry except with regard to the all

Although the exocrine glands of ants and other arthropod predators (150). Birds frequently prey on other bugs to spray birds (133). Rejection of Heteroptera is shown for the cardenolide mantids learn to avoid in cyanogenic rhopalids (8). Aposematic heteropterans frequently indicate that sequestration is more prevalent than camouflage.

Coincidence of aposematic norm for Heteroptera (4, 10) by alarm pheromones released (109, 112, 128) and reform (106). The lactonic excretory (2, 45) is an aggregation pheromone (unpublished). Other physical Heteroptera are unrelated to proves growth in seed-feeders (62), and leaf-feeding lacewings; however, feeding clusters on fruits (58). Congregated bugs are vulnerable than individual.

Parasitoids are also emitted. Secretions seem impotent. (39), yet feeding bugs are. There are even mites that reduviids limit parasitism by masses by covering them. The rectal gland of harpactocorids on stilt bug larvae might enhance crypsis because of. Mirid and tingid setal droplets in tingid droplets suggests that these exudates and parasitoids. (*E*)-2-Hexenal

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ants. The phenomenon whereby the model and the selective agent are the same (Wasmannian mimicry) was originally proposed to account for the morphological resemblance of myrmecophiles to ants. Although this is a dubious explanation for myrmecophile morphology, it may be a viable concept with regard to the allomones of Heteroptera (120).

Although the exocrine secretions of bugs are somewhat effective against ants and other arthropod predators (20, 127), they are ineffective against birds (150). Birds frequently prey upon Heteroptera, and the ability of coreids and other bugs to spray birds in the eyes confers only marginal protection (2, 133). Rejection of Heteroptera by birds is primarily based on taste (133), as shown for the cardenolide-sequestering Lygaeinae (51, 140, 141). Even mantids learn to avoid milkweed bugs (24). Reduction of the MTG in cyanogenic rhopalids (8, 29) and circumstantial evidence of countless aposematic heteropterans feeding on toxic plants (e.g. 58, 78, 103, 105, 132) indicate that sequestration or de novo synthesis (66, 161) of specific poisons is more prevalent than currently appreciated.

Coincidence of aposematic coloration with a tendency to aggregate is the norm for Heteroptera (4, 18, 55, 78, 80, 166). Aggregations may be dispersed by alarm pheromones released by aggravated larvae (27, 56, 99) or adults (82, 109, 112, 128) and reformed via aggregation pheromones (4, 18, 56, 80, 99, 106). The lactic excretory product of rhopalids in the genus *Jadera* (Figure 2, 45) is an aggregation pheromone for both adults and larvae (J. R. Aldrich, unpublished). Other physiological characteristics that favor gregariousness in Heteroptera are unrelated to aposematism. For example, group feeding improves growth in seed-feeding bugs (25, 58, 125), phloem-sucking coreids (62), and leaf-feeding lace bugs (162). Cotton stainer larvae appear aposematic; however, feeding clusters may deceive predators by mimicking flowers or fruits (58). Congregated bugs may avoid desiccation (100) and may be less vulnerable than individuals during molting (52).

Parasitoids are also enemies against which the MTG and larval DAG secretions seem impotent. Tachinid flies are major parasitoids of Heteroptera (39), yet feeding bugs are often oblivious to flies ovipositing on them (45). There are even mites that live inside the MTG of coreids (150). *Apiomerus* reduviids limit parasitism of their eggs to those on the periphery of their egg masses by covering them with resin (160). Volatiles from the female-specific rectal gland of harpactocorines (23) may repel egg parasitoids. Viscid droplets on stilt bug larvae might make it hazardous for parasitoids to oviposit and may enhance crypsis because berytids frequent plants with glandular hairs (171). Mirid and tingid setal droplets are not especially sticky, but the novel molecules in tingid droplets have nonpolar and polar ends (116, 117), which suggests that these exudates are allomones aimed at wetting small predators and parasitoids. (*E*)-2-Hexenol from the adult DAG secretion of the shield

bug *Hotea gambiae* is toxic to dipteran eggs and perhaps provides protection against tachinid eggs (69). Powdery wax on the sternae of some pentatomids (93) may make it difficult for tachinids to stick eggs onto these bugs. Indeed, the tachinid *Trichopoda plumipes* prefers to oviposit under the wings of *Brochymena* (50). Other biochemical, mechanical, and behavioral antiparasitoid adaptations surely exist, but one life-history strategy in Heteroptera that may be as important as any of these antiparasitoid defenses is the emission of long-range attractant pheromones by males rather than females.

REPRODUCTION

Attractant pheromones have been identified for only three bugs (10, 14, 21), but these prove that some heteropterans rely on pheromones to congregate. *Podisus* bugs are very generalized predators (105), and their attractants play a pivotal part in a polygynous mating system that is a conglomeration of resource defense, lek formation, and female defense (163). Overwintered females and males are attracted to calling males in spring before prey or parasites are abundant (3). The first-generation male initially searches for prey and then attracts a mate with his pheromone, thereby risking discovery by a complex of parasites (3, 10). Some males apparently avoid parasitism by not releasing pheromone and try to intercept females attracted to calling males. Regardless of season, copulation lasts much longer than necessary for sperm transfer; this common heteropteran trait has been interpreted as female defense (38, 104, 139).

Oligophagous pentatomoids seem more resource oriented than *Podisus*, yet the evidence still implicates males as the attractive sex. In *Nezara viridula* (21, 72, 121) and other pentatomoids of limited host breadth (110, 167), males attract females with a pheromone, thereby risking parasitization; this selects for a male counterstrategy. *N. viridula* males do not call per se; instead feeding appears to trigger pheromone synthesis and immediate release (30). In addition, tremulations sensed by vibroreceptors in the legs are exchanged during courtship, and rivalry signals warn males that attempt to intercede (41, 60). In asopines with pilose sternal patches, starvation followed by predation on preferred prey stimulates secretion (13, 16). Some scutellerids also emit male-specific exocines from pilose sternal patches (36, 89). Some pentatomids (163) and plataspids (75, 76) mate in aggregations at the same place for days, with individuals coming and going. The digestive advantage of group feeding (125) may have preadapted these insects to this scramble competition mating system (163). Males of one plataspid initiate aggregations because of sexual selection (75, 76), and plataspids are known to possess male-specific integumental glands (35, 108). The fruit juice-sucking marmorated stink bug *Halyomorpha mista* is an interesting exception to the picture just developed.

This bug has a large host range; both sexes are equally parasitoid (83).

Males of large phloeotomids (161, 163), and some seed bugs (161, 163), are defenders of resource. Males have ventral abdominal coreoid ventral abdominal secretions were unattractive to females. Males of these insects have a striped pattern on their abdomen. This fact, plus the striped pattern on the abdomen of males (5-15) to those of male lepidoptera, suggests that these glands during copulation mark mated females. A male mating pairs (5).

Reliance on poisons and chemical defense is a strong selection pressure on MTG to evolve (59, 92). Exocrine glands (36, 92) and sweet (92), and caged (126). In the cotton stink bug, the synthesis of the sex pheromone during courtship (73); this strong odd bit of circumstance may have a sexual role. Leg in the MTG (17) are of the same type.

Data for the remaining pheromones in these taxa are scarce because of the difficulty of studying them. In some predators (77) that form airborne pheromones and again males have been found to have characteristic reduviid pheromones that show up at carrying capacity. In *prolixus*, one report indicates more males than vice versa (126). In an airborne stimulant, males secrete a sex pheromone. Males in an olfactory test emit pheromone. Males identified from tarnished plant bug tests (74), but a minor role in corn silks and

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This bug has a large host range and is solitary except during hibernation. The sexes are equally parasitized by tachinids, and copulation only lasts about 10 min (83).

Males of large phloem-feeding coreids (11, 57, 62, 109), some lygaeid seed bugs (161, 163), and rhopalids that feed on poisonous Sapindaceae (38) are defenders of resources and females, and the males of most of these species have ventral abdominal glands (11, 164). An attractant role was proposed for coreoid ventral abdominal gland secretions (5), but blends mimicking these secretions were unattractive to *Leptoglossus* in the field. It is now known that males of these insects liberate sesquiterpenes (J. R. Aldrich, unpublished). This fact, plus the striking similarity of these coreid secretions (Figure 2, 5–15) to those of male lepidopterans and the fact that secretion oozes from the glands during copulation, suggests that ventral abdominal gland secretions mark mated females. At close range, *Leptoglossus* males are stimulated by mating pairs (5).

Reliance on poisons appropriated from plants has evidently relaxed selection pressure on MTG secretions of Lygaeinae (130), allowing sexual functions to evolve (59, 92). Lygaeine males possess at least one extra set of exocrine glands (36, 91, 164). Isolated *Oncopeltus fasciatus* males smell sweet (92), and caged milkweed bug adults attracted conspecifics in the field (126). In the cotton stainer, *Dysdercus koenigii*, juvenile hormone controls the synthesis of the olfactory signal from female MTGs that stimulates courtship (73); this strongly implicates linalool as the stimulant. One other odd bit of circumstantial evidence indicates that MTG secretions occasionally have a sexual role: Legume-feeding alydids that produce foul-smelling acids in the MTG (17) are often attracted to carrion and feces (122, 131).

Data for the remaining heteropteran infraorders give a sketchy outline of pheromones in these taxa. The meagerness of the data may be partially due to the difficulty of studying aquatic insects. Enicocephalids are scattered predators (77) that form airborne leks in the absence of defendable resources (159), and again males have hypertrophied exocrine glands (34). Isobutyric acid is a characteristic reduviid exocrine, and assassin bugs are among the few bugs that show up at carrion (122). For the blood-sucking reduviid *Rhodnius prolixus*, one report indicated that females are more attracted to the odor of males than vice versa (150). Another study showed that mating pairs produce an airborne stimulant attractive to males (150). *Triatoma mazzottii* females secrete a sex pheromone from sternites 6 and 7 that was attractive to virgin males in an olfactometer (118). For Miridae, all evidence indicates that females emit pheromones attractive to flying males (65a, 85, 158). Esters identified from tarnished plant bugs (67) were unattractive to the bugs in field tests (74), but a minor component from the bug, phenylacetaldehyde, is also found in corn silks and attracts *Lygus lineolaris* in the field (33).

MIGRATION

"To migrate is to use specialized behavior evolved for the displacement of the individual in space" (47). In insects, especially the Heteroptera, research on migratory specializations has focused on female emigration, the so-called oogenesis-flight syndrome, and on polymorphic and polyphenic variations in migratory capabilities (47). Mirids are vagile because they are strong fliers yet are small enough to ride wind currents (148). Mirid females attract males with a pheromone, and this must be considered a specialized behavior facilitating immigration. Another example of specialized displacement behavior in Miridae is provided by the relatively large (6 mm) *Harpocera thoracica* females, which produce an excess of terpenyl acetates in the MTG (Figure 2, 74, 75). Males live for one week in May (149), when they can be trapped by the hundreds (148), but females live longer and disperse acrially before ovipositing in oak twigs.

Pentatomorphan males have evidently been favored as pheromone emitters, and their flight facility is usually lifelong, but females often lose the propensity or ability to fly after the onset of oogenesis (47, 58, 111). Prolonged flight and the longer life span of male bugs have been interpreted solely as adaptations for locating mates (47). In fact, careful monitoring of immigration bouts showed that males are often the first arrivals at maturing seed crops (22, 31, 61). Furthermore, *Eurygaster integriceps* males only emit their vanillalike scent after migrating back to wheat fields in the spring (173). In various true bugs, adverse conditions increase larval mortality of females (25, 46), in effect leaving more male colonizers. In these and other heteropteran species, attractant pheromones are probably an important component of the colonization process.

CONCLUSIONS

Heteroptera seem to have a hodgepodge of independently evolved exocrine glands. When it comes to pheromone analysis, one way out of this semiochemical quagmire is to trap and characterize the airborne chemical signals. Even this method is fraught with the difficulty of herding bugs into a suitable apparatus without eliciting a chemical discharge. There are huge gaps in our knowledge of the semiochemistry of the group. Most investigations of heteropterans emphasize either chemistry or behavior but not both. Most taxa have yet to be examined, and the lack of information is especially acute for the important predators among the Nabidae, Anthocoridae, and Geocorinae. Even so, it is evident that parasitoids are powerfully attracted to the pheromones of Heteroptera, and pheromones could be immediately useful in locating parasitoids of exotic pests. The realization that some hymenopteran

parasitoids of Heteroptera may explain past failures in keeping track of the invaluable clues to the heteropteran crop pests and tools. Finally, elucidation of feeding bugs may lead to

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parasitoids of Heteroptera are phoretic and parasitize only freshly laid eggs may explain past failures and temper future efforts in biocontrol. Merely keeping track of the incidence of parasitism in each sex could provide valuable clues to the existence of new pheromones. As pheromones of heteropteran crop pests are identified they will find applications as monitoring tools. Finally, elucidation of chemical messengers for predatory and weed-feeding bugs may lead to pheromonal husbandry of these beneficial insects.

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BIOLOGICAL PEST CONTROL

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Research Station for Fruit

INTRODUCTION

The total world area of 150,000 ha; Table 1) cropping system have reasons. Few special possible to employ natives and ornamentals is not tolerated. Success damage from insects may cause fewer negative control is more effective example, pest control production (52); thus, although chemical application of biological in greenhouses is also introducing natural enemies resulted in extensive chemical control works; and ment and extension with use of information on